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Biomass and Compositional Characteristics of Kaneohe Bay, Oahu, Hawaii, Phytoplankton Inferred from Regression Analysis[1]

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ABSTRACT: Concentrations of chlorophyll *a* (chl *a*), particulate carbon (PC), and particulate nitrogen (PN) measured on a weekly basis in the picoplankton and nano-plus-microplankton size fractions over a 2-yr period from 1986 to 1988 at a station near a former sewage outfall in Kaneohe Bay, Oahu, Hawaii, were compared to similar data collected in 1970, 1972, 1974, and 1976–1977 while sewage was being discharged into the bay, and in 1978–1979 immediately after diversion of the sewage. Particulate concentrations showed considerable temporal variability both within and between years. High concentrations were associated with periods of above-average rainfall. Heavy rains that occurred during two successive periods of spring tides produced chl *a* concentrations of over 40 mg m^{-3} in January 1988, almost four times the highest concentration measured during the period of sewage discharges. Nutrients from land runoff as well as from decomposition of organisms killed by salinity stress were the apparent cause of this spectacular bloom. The bloom consisted almost entirely of nanoplankton and microplankton, but picoplankton accounted for 45 $\pm$ 14% of the chl *a* during the remainder of the 1986–1988 study. Phytoplankton C:N ratios were apparently unaffected by diversion of sewage from the bay and averaged within 10% of the Redfield ratio. This result implies that phytoplankton were growing at close to nutrient-saturated rates both before and after the sewage diversion. Nutrient budget calculations indicated that most of the growth has been supported by recycling within the bay. Phytoplankton C:chl and N:chl ratios estimated by regression analyses increased after the sewage diversion, apparently in response to the increase in average irradiance in the water column caused by the decline in seston concentrations. C:N ratios of picoplankton and nano-plus-microplankton under nutrient-saturated conditions were about 4.6 $\pm$ 0.3 and 6.2 $\pm$ 0.8, respectively; the difference probably reflected the high concentration of nitrogen-containing pigments in some picoplankton.

POINT SOURCE discharges of industrial wastewaters and sewage effluent into aquatic systems often introduce nutrients into the environment in quantities sufficient to noticeably accelerate the natural eutrophication process. The initial beneficiaries of such nutrient additions are the algae, and the nature of competition is such that phytoplankton are generally favored over benthic algae as the degree of nutrient enrichment increases (Hansson 1988). Phytoplankton may thus serve as sensitive indicators of trophic state.

Conceptually, phytoplankton response to nutrient enrichment may be in two ways, by a change in growth rate or by a change in biomass (Caperon et al. 1971). When limiting nutrient concentrations are sufficiently high, relative growth rates as defined by Goldman (1980) are close to 1.0, and further nutrient enrichment will produce a response from the phytoplankton almost entirely in the form of a biomass change and may favor species with higher absolute growth rate (μ_{max}). When rela-

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tive growth rates are low, the response of the phytoplankton to nutrient enrichment may be expressed as significant changes in growth rate or biomass, or both, with the relative importance of the two responses determined by interactions between components of the microbial food web. To evaluate the impact of cultural eutrophication on aquatic systems, it is therefore of interest to be able to measure changes in both phytoplankton biomass and relative growth rate.

Phytoplankton biomass is most frequently measured in terms of cholorophyll *a* (chl *a*) concentration, in part because chl *a* is associated uniquely with plants and in part because the measurement can be made easily and quickly. Relative growth rate (μ_r) is defined as the ratio of the actual growth rate to the growth rate under nutrient-saturated but otherwise identical conditions. Relative growth rates cannot be measured directly, but can be estimated indirectly from a knowledge of phytoplankton compositional characteristics. For that purpose the carbon-to-nitrogen ratio (C:N) in the phytoplankton is probably the most useful compositional characteristic because its relationship to μ_r seems to be highly insensitive to irradiance (Goldman 1986). Phytoplankton C:N ratios vary from about 5.7 by weight at $\mu_r = 1$ to 18.7 at $\mu_r = 0$ (DiTullio and Laws 1983, 1986). Carbon-to-chl *a* ratios (C:chl) are also highly correlated with μ_r, but the relationship is affected by irradiance and photoperiod (Goldman 1980). Comparisons of μ_r based on C:chl ratios are therefore most informative when light regimes are similar.

Estimating phytoplankton C:N and C:chl ratios in the field is confounded by the fact that seston includes particles other than phytoplankton. Often phytoplankton contribute only a small fraction of the particulate carbon (PC) and particulate nitrogen (PN) in the water column (Laws et al. 1984). The problem of obtaining accurate phytoplankton C:N and C:chl ratios could be solved if phytoplankton could be separated from the rest of the seston, and although several methods exist for accomplishing this task (e.g., flow cytometry, size fractionation, micromanipulation), no approach is without significant limitations (Eppley et al. 1977). Measurement of cell dimensions under the microscope combined with empirical equations relating cell size to carbon content (Mullin et al. 1966, Strathmann 1967) have sometimes been used to estimate phytoplankton carbon content, but the procedure is tedious and subject to several criticisms (Banse 1977), although Eppley et al. (1977) regarded this method as the most reliable in a comparison of seven indirect methods for estimating C:chl ratios in California coastal waters. Several approaches to estimating phytoplankton carbon content using incubations with C-14 have been used (Eppley 1968, Redalje and Laws 1981, Laws 1984), but none provides an estimate of phytoplankton nitrogen content.

One of the simplest methods for estimating phytoplankton compositional characteristics is to regress PC or PN against chl *a* and to interpret the slope of the regression line as the C:chl or N:chl ratio, respectively (Caperon et al. 1976). The phytoplankton C:N ratio can then be equated to the ratio of the two slopes. The validity of this approach rests on the assumptions that the C:chl and N:chl ratios are constant during the study period and that the concentration of nonplant seston is either constant or, if variable, uncorrelated with chl *a*. Banse (1977) has provided a thoughtful discussion of the limitations of this method. The approach is least subject to error when phytoplankton cells account for a large percentage of the seston. Under those conditions changes in phytoplankton carbon and nitrogen are expected to dominate changes in PC and PN, respectively, and a high degree of correlation is expected between chl *a* and both PC and PN.

One previously overlooked source of systematic error in the regression analysis method is the fact that a Model II rather than Model I regression is required in cases where neither the *X* nor *Y* variable is under the control of the investigator (Laws and Archie 1981). Field measurements of PC, PN, and chl *a* clearly fall into the category of uncontrolled observations. When Model I regression theory is incorrectly applied to a data set requiring a Model II analysis, the calculated slope of the regression line will be "lower in absolute value than the true slope of the functional relation-

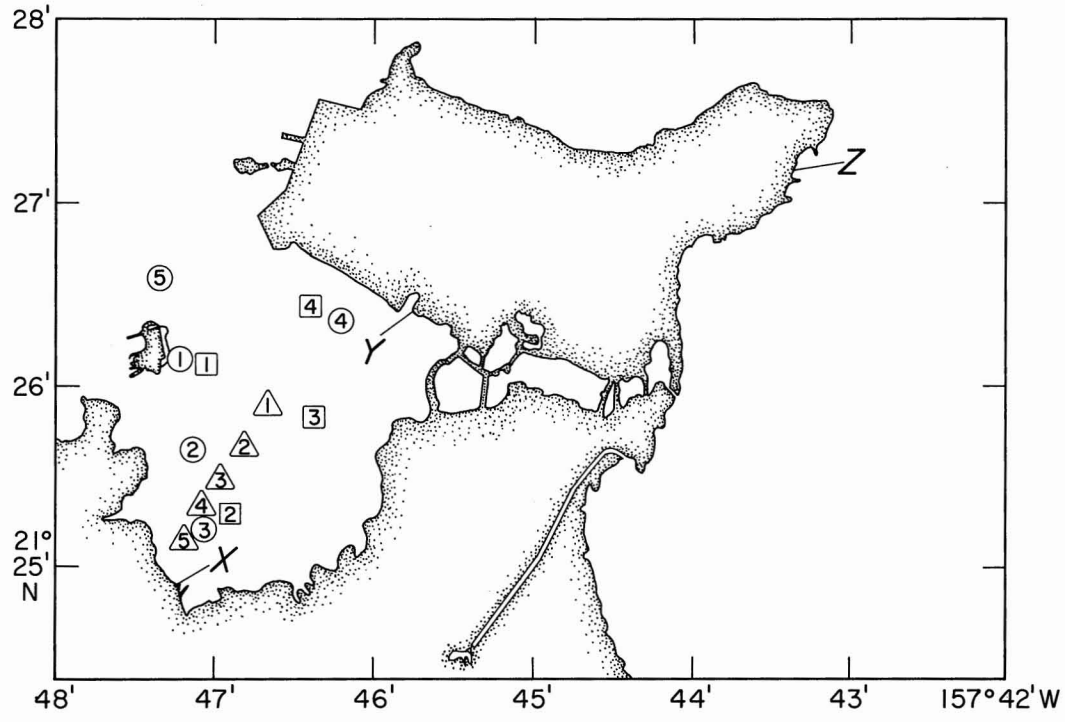

FIGURE 1. Location of sampling stations in the SE sector of Kaneohe Bay. The numbered circles, squares, and triangles represent stations sampled in spring 1970, fall 1972, and summer 1974, respectively. Sampling during 1976–1979 was conducted at 1970 station 2 and 1974 station 1. Sampling during 1986–1988 was conducted at 1972 station 2. X, Y, and Z mark the locations of the Kaneohe Municipal, Marine Corps Air Station, and Mokapu Point sewage outfalls, respectively.

ship" (Sokal and Rohlf 1969:482). The only exception to this statement is the case in which the product-moment correlation coefficient between X and $Y = \pm 1.0$.

The studies reported here were carried out in the southeast (SE) sector of Kaneohe Bay, a coastal embayment on the windward (northeast) side of the island of Oahu, Hawaii (Figure 1). Beginning in 1951, the SE sector of the bay was the recipient of increasing amounts of domestic sewage discharges, first from the Kaneohe Marine Corps Air Station and later (1963) from the town of Kaneohe (Figure 1). The loading of sewage increased from about 10^3 m^3d^{-1} in 1951 to 1.8×10^4 m^3d^{-1} in 1977, and after 1971 all of the sewage received secondary treatment (Smith et al. 1981). The cultural eutrophication that resulted from these discharges led to a serious deterioration of the coral reefs within the bay, and largely as a result of that fact the discharges were diverted to an ocean outfall off Mokapu Point in 1977 (Figure 1). Characteristics of the phytoplankton community reported by Caperon et al. (1976) reflect the increasing eutrophication of the bay from 1970 to 1974, and fortnightly sampling by Laws and Redalje (1979, 1982) during 1976–1979 provided information on the characteristics of the phytoplankton community during the 2.5 yr immediately preceding and 2 yr following the sewage diversion. Although chl *a* concentrations declined by almost a factor of two as a result of the sewage diversion, the decline was less than that expected from simple box model calculations. Fluxes of nutrients from the sediments and the decomposition of an estimated 400 tonnes of benthic organisms, primarily filter feeders, were suggested as the most likely cause of the less-than-expected decline in chl

a (Laws and Redalje 1982). Flushing of the bay with offshore water and the gradual depletion of nutrient reserves in the sediments were expected to further reduce the chl *a* concentrations in the years following the diversion.

In 1986–1988, 10 yr after the sewage diversion, weekly sampling was conducted in the SE sector to examine certain characteristics of the phytoplankton and other seston and to compare results with conditions reported during the period of cultural eutrophication and the year immediately after diversion of the sewage outfalls. The focus of this report is the results and implications of regression analysis of PC and PN on chl *a*, an approach emphasized in the earlier studies of Caperon et al. (1976). The 2-yr fortnightly and weekly time series in 1976–1978 and 1986–1988, respectively, also afforded an opportunity to examine temporal patterns in the data and to correlate those patterns with environmental conditions. Finally, size fractionation work conducted during the 1986–1988 study allowed us to compare the biomass and compositional characteristics of the picoplankton (0.2–2.0 μm) and nano-plus-microplankton less than 183 μm in size.

MATERIALS AND METHODS

Mehods used during the 1970–1974 and 1976–1978 studies were reported by Caperon et al. (1976) and Laws and Redalje (1979, 1982). We include here a brief summary of the earlier methods as well as those used during the 1986–1988 study.

During 1970 three samples per month were collected from a depth of 1 m during the March–May period at five locations in the SE sector of the bay. The water was prescreened through 0.33-mm Nitex netting to remove large zooplankton. Samples for PC and PN analysis were filtered onto Selas Flotronics silver filters (1.2 μm) and analyzed on a Hewlett-Packard model 185 CHN analyzer following procedures recommended by Gordon (1969). Samples for chl *a* analysis were collected on Whatman GF/C filters (1.2 μm), extracted in 90% acetone, and analyzed for chl *a* using the trichromatic equations of Strickland and Parsons (1968).

During 1972 six weekly cruises were conducted to four stations in the SE sector (Figure 1) between 15 September and 20 October. The samples were collected from a depth of 1 m and processed by methods identical to those used in 1970.

During 1974 samples were collected from a depth of 3 m at a total of five stations (Figure 1) during the period 14 May to 23 August. A total of 18 samples was collected, of which seven were taken at station 4, three or four at stations 1, 3, and 5, and one at station 2. All sample were prescreened through 0.102-mm Nitex netting and then filtered onto GF/C filters. The PC and PN analyses were performed using procedures recommended by Sharp (1974). Chl *a* analyses were performed as in 1970.

During 1976–1979, samples were collected from a depth of 1 m using a modified bilge pump fitted with an ordinary garden hose at two stations (Figure 1) on a fortnightly basis. The samples were prescreened through 0.202-mm Nitex netting and then processed as in 1974 except that the chl *a* samples were extracted in 100% acetone (Jeffrey 1974), the chl *a* concentrations were calculated using the trichromatic equations of Jeffrey and Humphrey (1975), particulate inorganic carbon (PIC) was determined using the method of Hirota and Szyper (1975), and analyses of PIC, PC, and PN were performed on a Hewlett-Packard model 185B CHN analyzer.

During the 1986–1988 fieldwork, samples were collected on a weekly basis at one station (Figure 1) from a depth of about 0.1 m using a Nalgene bottle that was opened only after it had been submerged. All samples were prescreened through 0.183-mm Nitex netting. Subsamples were filtered onto either Whatman GF/F (0.7 μm) or 2.0-μm Nuclepore membrane filters. Filtrate from the 2.0-μm Nuclepore filters was filtered onto GF/F filters. The GF/F filters were analyzed for PN, PC, and (during 1987–1988) PIC concentrations on a Hewlett-Packard model 185B CHN analyzer. Picoplankton PC and PN were assumed to be contained in the 2.0-μm Nuclepore filtrate that was retained on a GF/F filter. Nano-plus-

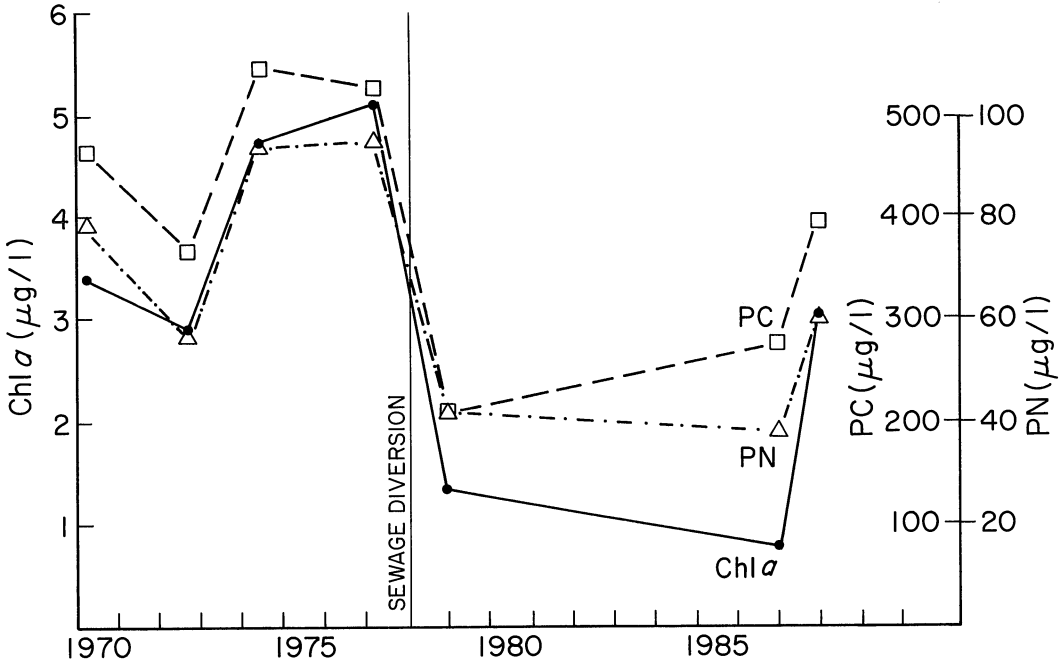

FIGURE 2. Average concentrations of chl *a*, PC, and PN during the seven sampling intervals from 1970 to 1988.

microplankton chl *a* was equated to the chl *a* retained on a 2.0-μm Nuclepore, and picoplankton chl *a* was equated to the difference between total chl *a* (GF/F) and nano-plus-microplankton chl *a*. Chl *a* analyses were performed on a Turner Model III fluorometer following the procedures of Holm-Hansen et al. (1965).

RESULTS

The average concentrations of chl *a*, PC, and PN measured during the various study periods are shown in Figure 2. Before the diversion of the sewage outfalls, substantial gradients existed in the concentrations of all three parameters within the SE sector (Laws and Redalje 1979). Therefore, comparison of results from the 1970, 1972, and 1974 studies required selection of a site that was more-or-less common to all three studies. Examination of Figure 1 shows that the only site common to all three studies was the immediate vicinity of Kaneohe municipal sewage treatment plant outfall. Data from the other stations sampled during the prediversion studies were therefore ignored in computing these averages. The studies in the year immediately following the sewage diversion included two sampling sites, one of which was in the vicinity of the old Kaneohe outfall, and values from that location were used in computing the averages in Figure 2. However, gradients of chl *a*, PC, and PN were much smaller in the SE sector after the diversion, and the averages from the 1978–1979 studies would have changed by less than 5% if data from both sampling sites (Figure 1) had been combined.

Although chl *a*, PC, and PN values declined dramatically in the year after the sewage diversion, the mean concentrations of all three were actually higher in 1987–1988 than in the fall of 1972. The cause of this surprising result can be traced to the temporal variability of the system. The fall 1972 studies were conducted over a period of only 1 month. It is apparent from Figure 3 that dramatic differences in mean concentrations can occur even when values are averaged over time periods as long as 3

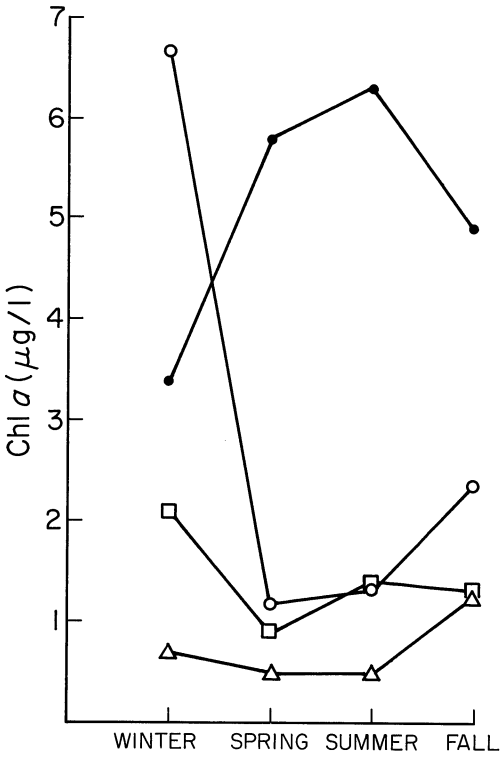

FIGURE 3. Seasonal averages of chl *a* during the four year-long sampling intervals. Solid circles, squares, triangles, and open circles represent seasonal averages in prediversion, postdiversion, 1986–1987, and 1987–1988, respectively.

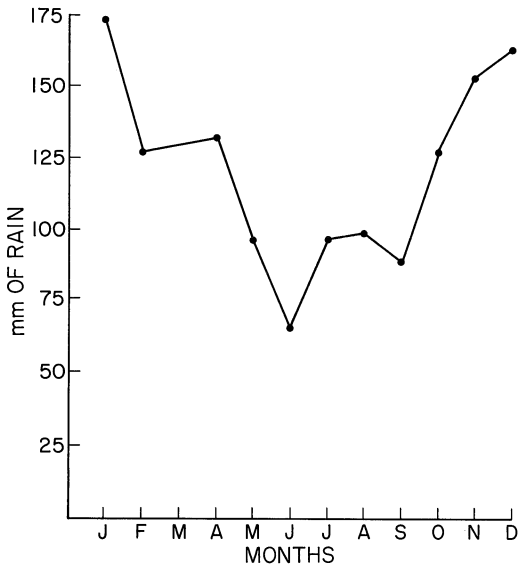

FIGURE 4. Average monthly rainfall at State of Hawaii Department of Land and Natural Resources rainfall station Kaneohe mauka during the period 1928–1983.

months. The usual pattern is for chl *a*, PC, and PN to peak during the fall and winter rainy season, when nutrient inputs from stream runoff reach a maximum, and to be at a minimum during the dry spring and summer months (Figure 4). However, in the year preceding the sewage diversion the peak concentrations occurred in the summer and the lowest concentrations in the winter. The unusual pattern in chl *a* concentrations was associated with the fact that rainfall during the year preceding the sewage diversion was almost twice as great during the spring and summer months (mean = 151 mm/month) as during the fall and winter (mean = 81 mm/month). Similarly, the very high chl *a* concentrations during the winter of 1988 are associated with unusually heavy rains that fell during November 1987–January 1988. During that time rainfall averaged 399 mm/month. Because of the observed temporal variability, concentrations averaged over time periods as long as several months to a year can give a misleading picture of the impact of perturbations such as the diversion of the sewage outfalls on the behavior of this system.

The results of the regression analyses of PC and PN on chl *a* are shown in Table 1 and Figures 5–7. Data from all the sampling stations shown in Figure 1 were included in the analysis. In the case of the 1970 and 1974 data, the regressions were performed on the average values for each of the stations, because the Model I equations published by Caperon et al. (1976) for those data sets do not satisfy the constraint equation $Y_{av} = a + b\ X_{av}$, where Y_{av} and X_{av} are the average values of the Y and X variables, respectively, and a and b are the regression intercept and slope, respectively.

The bloom that occurred during the winter of 1988 produced chl *a* concentrations as high as 41 mg m^{-3} on 12 January. During the roughly 6-week period of the bloom (22 December 1987–2 February 1988), the relation-

TABLE 1

RESULTS OF REGRESSION ANALYSIS OF PC AND PN ON CHL *a* USING MODEL II GEOMETRIC MEAN REGRESSION TECHNIQUES[a]

STUDY	REGRESSION	*R*
Spring 1970		
	PC = 22.4 + 124 chl *a*	0.939
	PN = 4.7 + 20.4 chl *a*	0.970
Fall 1972		
	PC = 35.4 + 124 chl *a*	0.790
	PN = 8.97 + 15.2 chl *a*	0.838
Summer 1974		
	PC = 221 + 67.4 chl *a*	0.994
	PN = 27.6 + 14.1 chl *a*	0.995
Prediversion (24 September 1976–28 October 1977)		
	PC = 161 + 71.3 chl *a*	0.817
	PN = 25.7 + 13.5 chl *a*	0.710
Postdiversion (2 June 1978–15 June 1979)		
	PC = 69.7 + 113 chl *a*	0.512
	PN = 10.1 + 24.7 chl *a*	0.557
13 May 1986–5 May 1987		
	PC = 148 + 162 chl *a*	0.723
	PN = 16.3 + 27.3 chl *a*	0.706
12 May 1987–26 April 1988 (excluding winter bloom)		
	PC = 101 + 117 chl *a*	0.660
	PN = 9.7 + 22.4 chl *a*	0.626
22 December 1987–2 February 1988 (winter bloom)		
	PC/chl *a* = 104 ± 23 (n = 7)	
	PN/chl *a* = 17.5 ± 6.2 (n = 7)	

[a] Concentrations are mg m^{-3}.

ships between chl *a* and both PC and PN appeared to be different from the relationships that prevailed during the remainder of the year. On six of seven occasions during the bloom, the measured concentrations of PC and PN were less than the corresponding values predicted from the regression line fit to the remaining data points. We therefore excluded the values measured during the bloom period from the data set used to calculate the regression lines for the period 5 May 1987–26 April 1988 (Table 1). Because chl *a* values were so high (average = 12.0 mg m^{-3}) during the bloom, we assumed that almost all the seston consisted of phytoplankton cells at that time and have therefore reported simply the mean PC : chl *a* and PN : chl *a* ratios during the bloom in Table 1.

To be consistent with the earlier studies of Caperon et al. (1976), we did not subtract PIC from our PC values. The extent to which our analyses were influenced by PIC may be ascertained by examining mean PIC concentrations and the correlations between PIC and chl *a*. For example, during the prediversion and postdiversion study periods, PIC concentrations averaged 72 and 23 mg m^{-3}, respectively, or 11–14% of the mean PC during

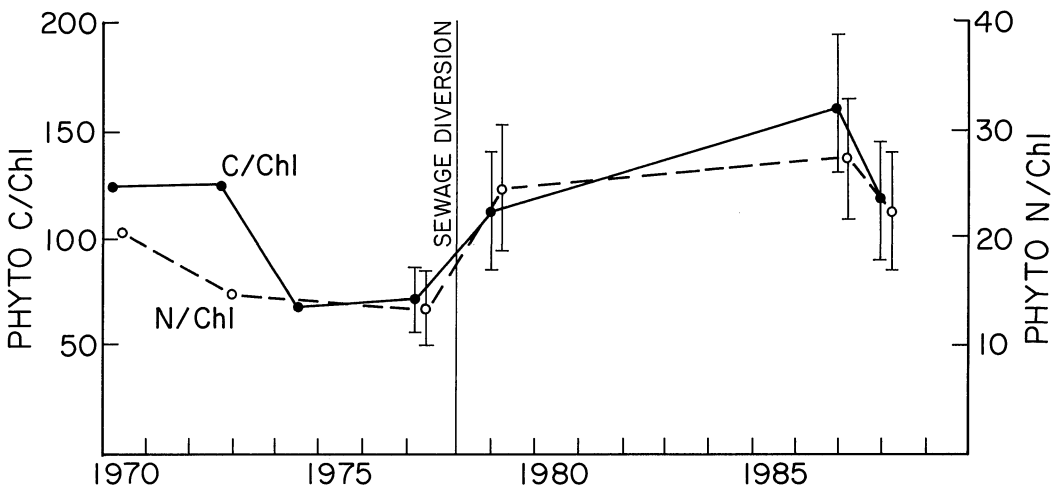

FIGURE 5. Ratios of phytoplankton C : chl *a* and N : chl *a* inferred from regression analysis during the seven sampling intervals. Error bars are 95% confidence intervals to the Model II regression slopes. Confidence intervals unavailable for 1970–1974 data.

the corresponding study periods. The correlation coefficients between PIC and chl *a* during the prediversion and postdiversion studies were −0.19 and 0.16, respectively, both statistically nonsignificant ($P > 0.10$). We conclude that the slopes of our regression lines were influenced very little by PIC and that most of the PIC appeared as a component of the regression intercepts. This conclusion and the nature of the ecosystem suggest that most of the PIC consisted of calcium carbonate carbon derived from the coral reefs in the bay.

The phytoplankton C:chl *a* and N:chl *a* ratios shown in Figure 5 are simply the slopes of the regression lines in Table 1. The phytoplankton C:N ratios shown in Figure 6 were calculated from the quotient of the C:chl *a* and N:chl *a* ratios in Figure 5. Nonphytoplankton PC was equated to the intercept of the PC versus chl *a* regressions in Table 1. Phytoplankton carbon in Figure 7 was calculated from the product of the mean chl *a* concentration during the particular study period and the corresponding slope of the PC versus chl *a* regression line.

Because of the high degree of temporal variability in the data sets from 1976–1979 and 1986–1988, a simple runs test was used to determine if the sequence of chl *a*, PC, and PN values followed a nonrandom pattern. The number of runs above and below the median value in the time series was the criterion for deciding whether the pattern was nonrandom or not (Sokal and Rohlf 1969). Not surprisingly, if the time series from 1976–1979 were treated as a single data set, the pattern of values was highly nonrandom ($P < 0.005$), with far less than the number of runs associated with a random sequence of numbers. This result reflects the dramatic drop in chl *a*, PC, and PN between the prediversion and postdiversion year (e.g., Figures 2 and 7). However, if the prediversion and postdiversion years were analyzed separately, the number of runs was not significantly different

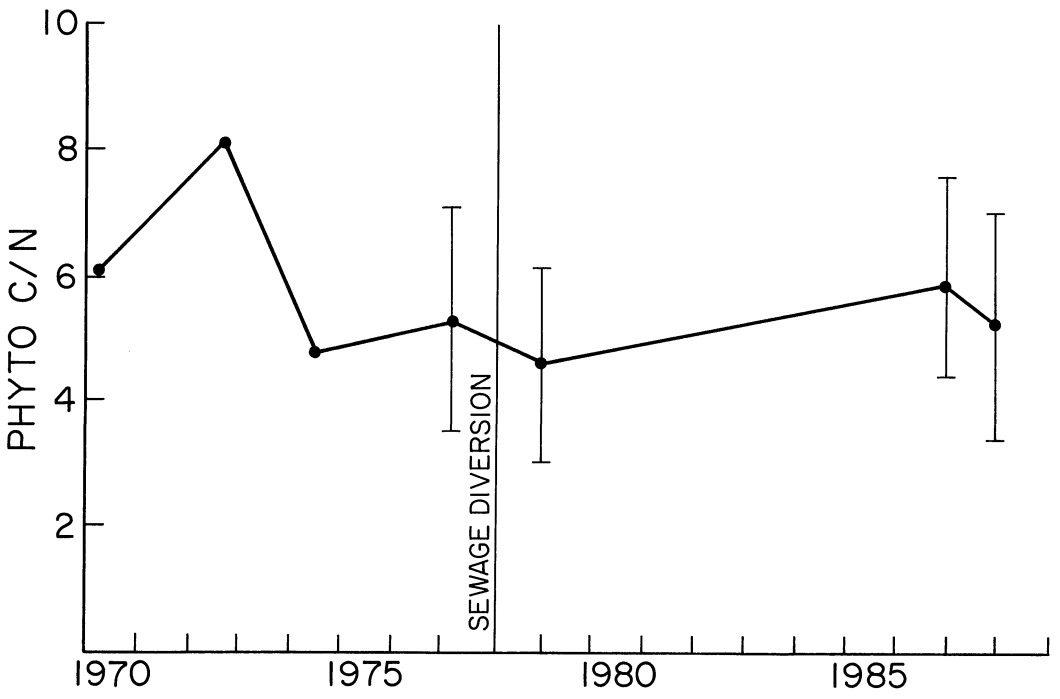

FIGURE 6. Phytoplankton C:N ratios calculated from the ratio of C:chl *a* and N:chl *a* estimates in Figure 5. Error bars are 95% confidence limits. Confidence intervals unavailable for 1970–1974 data.

($P > 0.05$) from that associated with a random sequence of numbers.

The results were quite different when the same runs test was applied to the data from 1986–1988. In both study years, there were far fewer than the number of runs expected for a random sequence of numbers ($P < 0.005$). This conclusion might have been expected for the 1987–1988 data because of the large bloom that occurred in the winter of 1988 (Figure 3). However, no comparable bloom occurred during the 1986–1987 period (Figure 3).

The results of the size fractionation studies during 1986–1988 proved revealing in several respects. With the exception of the 1988 winter bloom, picoplankton accounted for a rather constant percentage of 45 ± 14% of the chl *a* in our samples. However, picoplankton accounted for only 3% of the chl *a* at the peak of the bloom and for only 9 ± 5% of the chl *a* during the last 4 weeks of the bloom. Thus the bloom consisted almost entirely of nano- and microplankton. Regression analyses on the size fractions (Table 2) showed several trends. Phytoplankton C:chl *a* and N:chl *a* ratios were consistently lower in 1987–1988 than in 1986–1987, and nano-plus-microplankton C:chl *a* and C:N ratios were higher in both years than the corresponding picoplankton ratios.

DISCUSSION

Temporal Variability

Perhaps the most surprising result of this study was the high degree of temporal variability in chl *a*, PC, and PN concentrations. Subtropical embayments such as Kaneohe Bay are rightfully considered to experience a more stable environment than that of comparable ecosystems at higher latitudes. Nevertheless, it is apparent from data in Figure 3 that seasonal averages of chl *a* concentrations typically vary by at least a factor of two in Kaneohe Bay. Such temporal variation may obscure effects from treatments such as the diversion of sewage discharges (Figure 2) where the expected response is to change chl *a* values by a factor of two to three unless monitoring is conducted over a period of a year or more.

The amount of temporal variability evident in the 1987–1988 data (Figure 3) is undoubtedly atypical of this system and deserves further comment. Chl *a* values during the winter of 1988 reached a peak of 41 mg m^{-3}, a figure almost four times the highest concentrations measured during the 12-month prediversion study. It is remarkable that heavy rainfall could produce a response almost four times greater than that caused by the daily discharge

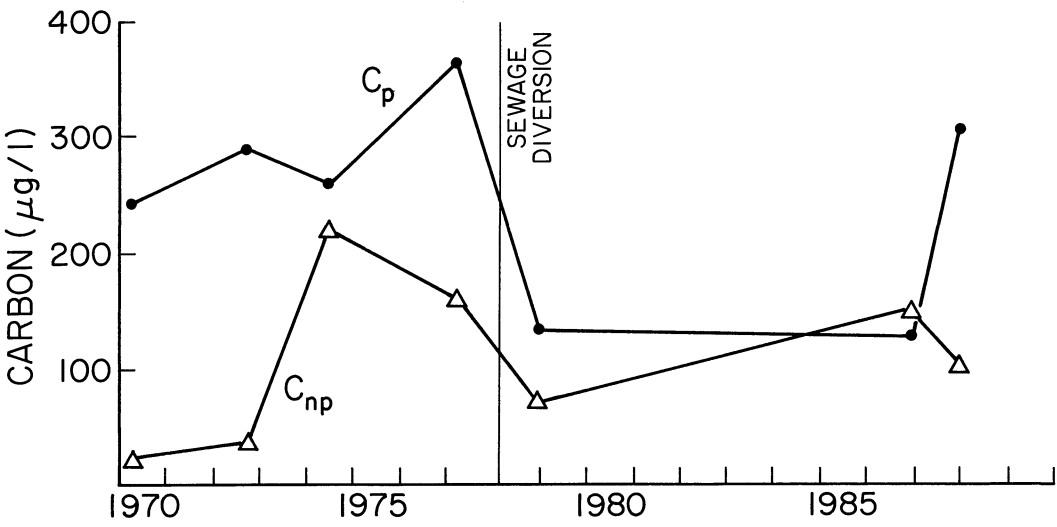

FIGURE 7. Phytoplankton carbon (C_p) and nonphytoplankton carbon (C_{np}) inferred from regression analysis during each of the seven time intervals.

TABLE 2

RESULTS OF SIZE FRACTIONATION STUDIES DURING 1986–1988 STUDIES

SIZE FRACTION	REGRESSION	R	PHYTOPLANKTON C:N
13 May 1986–5 May 1987			
Total			
	PC = 148 + 162 chl a	0.723	5.9
	PN = 16.3 + 27.3 chl a	0.706	
>2 μm (nano + microplankton)			
	PC = 79 + 191 chl a	0.760	7.0
	PN = 9.1 + 27.3 chl a	0.717	
<2 μm (picoplankton)			
	PC = 59 + 145 chl a	0.590	4.9
	PN = 6.5 + 29.6 chl a	0.480	
12 May 1987–26 April 1988 (excluding winter bloom)			
Total			
	PC = 101 + 117 chl a	0.660	5.2
	PN = 9.7 + 22.4 chl a	0.626	
>2 μm			
	PC = 69.1 + 128 chl a	0.695	5.5
	PN = 7.3 + 23.1 chl a	0.582	
<2 μm			
	PC = 48.1 + 80.7 chl a	0.526	4.3
	PN = 4.4 + 18.7 chl a	0.616	
22 December 1987–2 February 1988 (winter bloom; $n = 7$)			
Total			
	PC/chl a = 104 ± 23		5.9
	PN/chl a = 17.5 ± 6.2		
>2 μm			
	PC/chl a = 107 ± 24		6.2
	PN/chl a = 17.3 ± 9.1		
<2 μm			
	PC/chl a = 148 ± 65		4.5
	PN/chl a = 33 ± 16		

of 1.8×10^4 m^3 of secondary sewage effluent. The greatest amount of rain, about 418 mm, fell between 20 December 1987 and 3 January 1988. The bloom had begun to develop by 22 December 1987. However, comparable amounts of rain fell in February 1979 and November 1986, but chl a concentrations at those times peaked at only 3.5–4.0 mg m^{-3}. The greater impact of the December 1987–January 1988 rainfall was apparently due to the fact that most of the rain fell during spring tides. About 191 mm fell on a single day, 20 December 1987, when the tidal amplitude was the second highest of the calendar year. An additional 182 mm fell during 1–3 January 1988, also a period of spring tides. The reduction in salinity caused by freshwater runoff from that storm killed significant numbers of shallow-water fauna in the bay (T. Clarke, pers. comm.). The impact of the fresh water on reef biota was undoubtedly exacerbated by the fact that near-surface winds in Kaneohe Bay during the period 20–22 December were unusually calm, with a mean speed of only 5.7 km h^{-1} (L. Watteri, pers. comm.). Nutrients released from the decomposition of dead organisms probably added substantially to the nutrients introduced directly with stream runoff. Other freshwater kills have occurred on the Kaneohe Bay reefs from time to time in the past, the best documented example being the event of 2–3 May 1965, when almost 440 mm of rain fell within a period of 25 hr (Banner 1968), also at a time of near maximal spring tides. A similar combination of heavy rainfall and spring tides seems to have caused the freshwater kill of December 1987–January 1988 and the subsequent spectacular bloom of phytoplankton.

The results of the runs tests on the 1976–

1979 and 1986–1988 data provided additional insights concerning temporal variability within the bay. Despite the apparent seasonality in the prediversion data set (Figure 3), the runs test gave no evidence of a nonrandom sequence of values. Yet during 1986–1987, when seasonality was less evident, the runs test detected nonrandomness at a high level of confidence. The explanation for this apparent discrepancy is twofold. First, within a season there are usually substantial temporal variations in chl *a*, PC, and PN. Coefficients of variation as high as 50% are not uncommon for averages of these parameters over a 3-month period in our data. Hence, even though seasonal averages may seem to define a smooth curve (Figure 3), temporal noise greatly reduces the statistical significance of the apparent seasonal cycle. Second, the residence time of water in the SE sector of the bay is about 13 days (Smith et al. 1981). During 1976–1979 samples were collected on a fortnightly basis, and hence the water in the SE sector had a chance to turn over once between each sampling. However, during 1986–1988 sampling was conducted on a weekly basis. Hence there was only half as much time for the system to effectively flush out between samplings during the 1986–1988 study. The implication of the runs tests, therefore, seems to be not so much that there was more seasonality in 1986–1988 than in 1976–1979, but rather that the interval between sampling in 1986–1988 was sufficiently short that values measured on a given sampling date tended to be highly correlated with values measured on the previous sampling date.

Relative Growth Rate

Phytoplankton C:N ratios estimated from regression analysis were remarkably constant from 1974 to 1988 and averaged 5.2 ± 0.5. A C:N ratio of about 5.7 or less is associated with a μ_r of 1.0 (DiTullio and Laws 1983, 1986). The C:N of 8.2 estimated during the fall of 1972 would be associated with a μ_r of 55%. Based on this analysis, diversion of the sewage outfalls did not produce a significant change in the degree of nutrient limitation of phytoplankton growth rates in the bay. Growth rates appear to have been essentially unlimited by the supply of nutrients during all the study periods with the exception of the fall 1972 time interval. An independent check of this conclusion may be made using data reported by Taguchi and Laws (1987). They measured the percentage of C-14 incorporated into protein by phytoplankton in the bay on a weekly basis from January 1985 to January 1986. The average percentage was 47%, with a range of 41–54%. Based on the work of DiTullio and Laws (1983), the figure of 47% translates into a μ_r of 0.91, which is in reasonable agreement with our μ_r estimate of 1.0 based on C:N ratios derived from regression analysis. The implication of these two independent sets of observations is that phytoplankton growth rates in the bay are close to nutrient-saturated values.

This conclusion contradicts the earlier estimates of Laws and Redalje (1982), which suggested that μ_r values were only about 0.37 and 0.28 during prediversion and postdiversion conditions, respectively. However, those estimates were based on productivity estimates using C-14 and the assumption that nutrient-saturated growth rates (μ_m) in the bay were about 1.5 d^{-1}, or a little over two doublings per day. Although such growth rates are possible for particular species at temperatures (21–29°C) found in Kaneohe Bay (Eppley 1972), it seems doubtful that the entire phytoplankton community would be capable of turning over that rapidly. Experiments involving C-14 labeling of chl *a* and phytoplankton protein during 1982 led to the conclusion that μ_m for Kaneohe Bay phytoplankton is closer to 0.9 d^{-1} (Laws et al. 1984). Further, use of clean sampling and incubation techniques (Fitzwater et al. 1982) in conjunction with C-14 studies has raised primary production estimates in open ocean, coastal, and upwelling areas by factors of approximately 2.6, 2.5, and 1.4, respectively (Martin et al. 1987). Clean techniques were not used in the studies of Laws and Redalje (1979, 1982), and hence it would not be surprising if their primary production estimates were low by roughly a factor of two. Doubling their primary production estimates and assuming a μ_m of 0.9 d^{-1} causes their μ_r estimates to become 1.1 ± 0.2, in reasonable agreement with the values esti-

mated here and by Taguchi and Laws (1987). A simple nutrient budget calculation indicates that during prediversion conditions at least 70% of that rapid growth was supported by nutrient recycling and that during postdiversion conditions recycling supported over 90% of primary production (Laws and Redalje 1982).

Carbon: Chlorophyll a *Ratios*

Phytoplankton C:chl *a* ratios increased from 71 during the year immediately preceding the sewage diversion to an average of 131 during the three study years after the diversion (Figure 5). For comparative purposes, ratios of adenosine triphosphate (ATP) to chl *a* near the sewer outfall in the prediversion year averaged 0.227 by weight (Laws and Redalje 1979). If we assume that phytoplankton accounted for most of the ATP and that the C:ATP ratio in phytoplankton was about 311 (Laws et al. 1983), the C:chl *a* ratio is calculated to be (0.227) (311) = 71, identical to the value derived from our regression analysis. However, during the postdiversion year of 1977–1979, ATP:chl *a* ratios in the SE sector again averaged 0.227 (Laws and Redalje 1982), and the implied C:chl *a* ratio would again be 71, which is about 37% less than the regression slope estimate of 113 for that year (Table 1). Similarly, an estimate of phytoplankton carbon content based on C-14 labeling of chl *a* during August 1982 led to a C:chl *a* ratio of 84 (Laws et al. 1984).

The implication of these comparisons seems to be that the regression technique tended to overestimate C:chl *a* ratios after the diversion of the sewage outfalls. However, none of the three methods used to estimate C:chl *a* ratios is above criticism. The chl *a* labeling technique (Laws 1984) is probably the most accurate, but that method was used on only a single date in 1982. Given the temporal variability of biomass in the system, it seems inadvisable to attach great relevance to that single number. Laws et al. (1983) studied variability in marine phytoplankton C:ATP ratios and concluded that the ratio could differ from 311 by as much as a factor of two. Finally, even if all the assumptions underlying the use of regression analysis to estimate C:chl *a* ratios are satisfied, there is still considerable scatter in the 1978–1979 data set ($R = 0.512$), and the confidence limits on the slope are correspondingly large. Using Ricker's (1973) assumption that the confidence intervals for Model I and II regression slopes are about equal, the 95% confidence interval for the C:chl *a* ratio in 1978–1979 is about 85–141 (Figure 5). Hence from a statistical standpoint there is no convincing evidence that the three methods of estimating phytoplankton C:chl *a* ratios are yielding different answers.

Despite the scatter about the regression lines, C:chl *a* ratios derived from regression slopes appear to be significantly higher after the sewage diversion than during the prediversion study (Figure 5). A similar conclusion applies to the phytoplankton N:chl *a* estimates. What could be the cause of such a change in compositional characteristics? Phytoplankton C:chl *a* ratios are known to be negatively correlated with growth rates under nutrient-limited conditions (Goldman 1980, Laws and Bannister 1980), and an increase in C:chl *a* would therefore imply a decrease in growth rate. Although this explanation is logically appealing considering the fact that a major source of allochthonous nutrients disappeared in 1977–1978, several lines of evidence indicate that this explanation is incorrect. First, most production in the bay is supported by recycled rather than allochthonous nutrients (Laws and Redalje 1982). Biomass in the bay is undoubtedly controlled to a large extent by the supply of allochthonous nutrients (Figure 2), but growth rates are controlled primarily by internal recycling mechanisms. Second, C:N ratios, which are the best indicators of μ_r, were almost identical before and after the sewage diversion (Figure 6). Finally, N:chl *a* ratios are rather insensitive to the degree of nutrient limitation (Perry 1976). Hence one would not expect to see similar percentage changes in both C:chl *a* and N:chl *a* if differences in the degree of nutrient limitation were the cause of the shifts.

Irradiance is known to influence both C:chl *a* and N:chl *a* ratios, both ratios being positively correlated with irradiance (Laws and Bannister 1980, Geider 1987). However, the

relationship between phytoplankton C:N ratios and μ_r is very insensitive to irradiance (Goldman 1986). Given this information, a logical interpretation of the data in Figure 5 is that the average irradiance experienced by the phytoplankton in the bay increased after the sewage diversion. Evidence in support of this explanation is the fact the average Secchi depths near the sewage outfall increased from 3.1 ± 0.3 m during the year before the sewage diversion to 6.4 ± 1 m in the postdiversion year (Laws and Redalje 1979, 1982). If we take the depth of the SE sector to be 9.5 m (Laws and Redalje 1982) and the vertical extinction coefficient of light to equal 1.7 divided by the Secchi depth (Sverdrup et al. 1942), then this change in Secchi depth translates into about a 90% increase in the average irradiance in the water column. Such a change could certainly have caused the increase in C:chl *a* and N:chl *a* ratios apparent in Figure 5.

Contribution of Phytoplankton Carbon to Total Particulate Carbon

The relative importance of phytoplankton carbon (C_p) and other forms of PC in the seston is a subject of theoretical interest (Caperon 1975) and practical importance in the use of regression analysis to estimate phytoplankton compositional ratios (Caperon et al. 1976, Eppley et al. 1977). Although it was unclear how the regression equations published by Caperon et al. (1976) for those data sets were determined, their (1976) Model I regression equations for the 1972 data do satisfy the constraint equation and were therefore converted to Model II geometric mean equations. The Model II slope (B) was set equal to the Model I slope divided by the absolute value of the correlation coefficient, and the Model II intercept (A) was calculated from the equation $A = Y_{av} - BX_{av}$. Figure 7 shows the amounts of C_p and nonphytoplankton carbon (C_{np}) near the sewage outfall during the seven sampling intervals discussed in this report. During the spring 1970 and fall 1972 studies C_p accounted for about 90% of the PC, but during the last five sampling intervals this percentage dropped to a rather constant value of 62 ± 12%. There are several independent checks on this figure. Multiplying the ATP concentrations of Laws and Redalje (1979, 1982) by 311 to estimate C_p produces C_p:PC ratios of 0.64 and 0.38 during the studies of 1976–1977 and 1978–1979, respectively. An estimate of C_p by C-14 labeling of chl *a* in August 1982 produces a C_p:PC ratio of 0.64 (Laws et al. 1984). Based on these independent estimates it seems reasonable to conclude that C_p probably accounts for 50–70% of PC on the average in this system. The low estimate of 38% obtained by multiplying ATP:PC ratios from the 1978–1979 study by 311 may simply reflect an underestimation of the C:ATP ratio in the phytoplankton during that time, a possibility noted in the discussion of C:chl *a* ratios.

The fact that phytoplankton carbon apparently accounts for more than half the PC in this system explains in part the success of the regression technique in estimating phytoplankton compositional ratios. The regression approach is much less successful in systems such as the open ocean, where phytoplankton may account for less than 10% of the particulate matter in the euphotic zone (Glibert et al. 1985), because in such systems the scatter of points about the regression line may result in a slope and intercept of little or no statistical significance (Caperon et al. 1976). Based on Caperon's (1975) trophic level model of the Kaneohe Bay water column community, we had expected to see a decrease in the C_p:PC ratio after the sewage diversion and a concomitant decrease in the correlation coefficients between chl *a* and both PC and PN. The latter expectation seems to have been fulfilled. Ignoring the spring 1970 and summer 1974 regressions, which were fit to station means rather than to raw data, the correlation coefficients in Table 1 average 0.79 ± 0.06 and 0.63 ± 0.08 before and after the sewage diversion, respectively. A decrease in the C_p:PC ratio is more difficult to demonstrate. If the C_p:PC ratios from the four time intervals before the sewage diversion are simply averaged, the mean is 0.76 ± 0.18, and the mean C_p:PC ratio from the three postdiversion studies is 0.62 ± 0.15. The difference between the two means is not significant (t test, $t = 1.09$; df = 5; $P > 0.05$). The data from 1976–1988 are influenced by the 1988 winter bloom, which as

already noted was a very unusual occurrence. If the data from the bloom period are ignored, the C_p:PC ratio for 1987–1988 drops from 0.75 to 0.64, but the mean for the three post-diversion time intervals is 0.59 ± 0.11, still not significantly different from the prediversion mean of 0.76 ± 0.18. In summary, the data suggest a drop in the C_p:PC ratio after the sewage diversion in accord with expectation (Caperon 1975), but the difference is not statistically significant.

Picoplankton

Our final comments concern the role and physiology of picoplankton and nano-plus-microplankton in this system. The importance of picoplankton in both marine and freshwater systems has received a great deal of attention in recent years (Fogg 1986, Stockner and Antia 1986, Platt and Li 1987), and it seems fair to say that these tiny and previously overlooked organisms are now regarded as contributing a significant percentage of the primary production and biomass in many aquatic systems. Because of their large surface-to-volume ratios, picoplankton seem to be well suited to compete for nutrients where concentrations are low, and indeed most reports of their abundance come from oligotrophic environments (Stockner and Antia 1986). It was therefore of some interest to us to discover that picoplankton accounted for an average of 45% of the chl *a* in Kaneohe Bay during the 1987–1988 study period, excluding the 1988 winter bloom. This average value is similar to one observed during the 1985–1986 period (Taguchi and Laws 1987). The average chl *a* concentration of 1.5 mg m^{-3} during that time would certainly rank the system as eutrophic, and our estimated C:N ratios (Figure 6) indicate that growth rates were close to nutrient-saturated values. However, it is noteworthy that the 1988 winter bloom was completely dominated by nano-plus-microplankton. The implication seems to be that the larger phytoplankton are able to outcompete picoplankton when nutrients are supplied in a large pulse, but that picoplankton can effectively compete with nano- and microplankton when the pulses are small and frequent (i.e., zooplankton excretion). In the former case competition might tend to favor the larger phytoplankton because of their greater ability to store nutrients. The tendency of net plankton to increase in importance relative to nanoplankton during bloom conditions is a well-documented phenomenon (Yentsch and Ryther 1959, Malone 1971, Hitchcock et al. 1987).

Table 2 provides some indication of the nutritional status of the picoplankton and nano-plus-microplankton in the bay. Picoplankton C:N ratios were consistently less than nano-plus-microplankton C:N ratios, and this fact might be interpreted to mean that picoplankton μ_r values were higher than those of the larger phytoplankton. However, the fact that this same condition prevailed during the 1988 winter bloom, when the bay received a large pulse of nutrients and picoplankton were clearly outcompeted by larger phytoplankton, tends to argue against this interpretation. An alternative explanation would be that the C:N ratio of picoplankton under nutrient-saturated conditions is actually somewhat less than the Redfield ratio of 5.7 (Redfield et al. 1963), perhaps because some members of the picoplankton contain large amounts of nitrogen-containing pigments (Alberte and Kirchman 1985). If this interpretation is correct, then the data in Table 2 suggest that the C:N ratios of picoplankton and nano-plus-microplankton at $\mu_r = 1.0$ are about 4.6 and 6.2, respectively, as suggested by the previous study of Taguchi and Laws (1987) using a technique of C-14 incorporation into protein.

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